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'Where' depends on 'what': A differential functional anatomy for position discrimination in one- versus two-dimensions

Gereon R. Fink [a,b,*], John C. Marshall [c], Peter H. Weiss [b], Nadim J. Shah [b], Ivan Toni [b], Peter W. Halligan [d], Karl Zilles [b,e]

[a] *Neurologische Klinik, Heinrich-Heine-Universität Düsseldorf, Düsseldorf, Germany*
[b] *Institut für Medizin, Forschungszentrum Jülich, 52425 Jülich, Germany*
[c] *Neuropsychology Unit, University Department of Clinical Neurology, The Radcliffe Infirmary, Oxford, UK*
[d] *School of Psychology, Cardiff University, Cardiff, UK*
[e] *C & O Vogt-Hirnforschungsinstitut, Heinrich-Heine-Universität Düsseldorf, Düsseldorf, Germany*

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Abstract

Line bisection is widely used as a clinical test of spatial cognition in patients with left visuospatial neglect after right hemisphere lesion. Surprisingly, many neglect patients who show severe impairment on marking the center of horizontal lines can accurately mark the center of squares. That these patients with left neglect are also typically poor at judging whether lines are correctly prebisected implies that the deficit can be perceptual rather than motoric. These findings suggest a differential neural basis for one- and two-dimensional visual position discrimination that we investigated with functional neuroimaging (fMRI). Normal subjects judged whether, in premarked lines or squares, the mark was placed centrally. Line center judgements differentially activated right parietal cortex, while square center judgements differentially activated the lingual gyrus bilaterally. These distinct neural bases for one- and two-dimensional visuospatial judgements help explain the observed clinical dissociations by showing that as a stimulus becomes a better, more 'object-like' gestalt, the ventral visuoperceptive route assumes more responsibility for assessing position within the object.

Keywords: Visuospatial; Neuroimaging; Judgement; Landmark task

1. Introduction

Line bisection has long been used as a clinical test for unilateral visuospatial neglect [14]. Although most studies implicate right inferior parietal cortex as a key structure [14,32], bisection errors are also observed after a range of other lesions sites [14,22,32]. Also, the mere fact of systematic line bisection errors after brain damage does not indicate which particular visuospatial functions are required for accurate task performance. For example, patients with typical line bisection errors following right temporoparietal lesions may show normal performance when they have to mark the center of a square [11,30]. This suggests that position discrimination in one- and two-dimensional space employs partially distinct neural mechanisms. A similar conclusion follows from perceptual judgement tasks. Patients with left neglect are typically poor at judging whether lines are correctly bisected [21], while patients with damage to a range of right posterior cortex regions, including occipito-temporal cortex, but no unilateral neglect can be seriously impaired at judging whether a dot is situated in the center of a square [36].

The current study exploits such neuropsychological dissociations by contrasting line center and square center judgements using fMRI to distinguish the brain regions responsible for basic perceptual aspects of posi-

* Corresponding author. Present address: Institut für Medizin, Forschungszentrum Jülich, 52425 Jülich, Germany. Tel.: +49-2461-612725; fax: +49-2461-612820.
E-mail address: g.fink@fz-juelich.de (G.R. Fink).

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tion estimation in one or two dimensions. Subjects were scanned while viewing outline squares (conditions 1 and 2) or lines (conditions 3 and 4). In conditions 1 and 3, subjects indicated by right hand button press whether or not the square (1: Squaremark task, SM) was correctly pre-marked in its center or whether or not the line (3: Landmark task, LM) was correctly pre-bisected. In conditions 2 and 4, subjects indicated by right hand button press whether or not there was a mark anywhere within the square (2: control for Squaremark task, SC) or anywhere on the line (4: control for Landmark task, LC). A low level visual baseline (in which no visuospatial task was performed) served to establish the neural basis common to all four conditions. The factorial design allowed us to assess the neural activations associated with the different stimuli (factor 1: SM + SC > LM + LC and vice versa), with both positional judgement tasks (factor 2: SM + LM > SC + LC), as well as the simple main effects of the Landmark (LM > LC) and Squaremark (SM > SC) tasks. Differential activations observed during the Landmark and Squaremark tasks were then tested for significance by assessing the interactions (SM–SC > LM–LC and LM–LC > SM–SC) of the activations elicited by the positional judgement tasks with the visual stimuli used (lines or squares). The different visual inputs inherent to the Squaremark and Landmark tasks are thus controlled.

In a previous fMRI study, we demonstrated the normal functional neuroanatomy of line center judgements [6]. These judgements of whether or not pre-transected lines were correctly bisected [24] were associated with increased neural activity in right parietal cortex centered on the intraparietal sulcus, in early visual processing areas bilaterally, the cerebellar vermis and the left cerebellar hemisphere [6]. Based on that study and the lesion literature [14,33], we expected to replicate activation of right inferior parietal cortex during the Landmark (better termed 'linemark') task. Because of the observed dissociation between position discrimination tasks involving lines versus squares in lesion studies [11,12,21,30,36], we hypothesized that square center judgements would not activate right parietal cortex but rather occipital regions involved in visual shape analysis and object processing [3,17,18, 20,27]. We emphasize that the design of this study does indeed isolate the operation of position discrimination per se after other task demands have been removed by subtraction of the control conditions. These control tasks involve visual detection of a mark (or its absence) within the prescribed spatial extent of a horizontal line or a square. What remains after the mark has been detected in the Landmark and the Squaremark tasks is simply to judge whether or not that mark is centrally positioned.

2. Methods

2.1. Subjects and experimental design

Twelve healthy, right-handed male volunteers were studied after obtaining written informed consent and approval by the local ethics committee. In conditions 1 and 2, squares with sides corresponding to visual angles of 10° (horizontal and vertical) or 12° (horizontal and vertical) were presented in black on a white background for 450 ms, with an interstimulus interval of 1050 ms in the center of the screen quadrants (each quadrant representing a horizontal visual angle of 30° and a vertical visual angle of 15.5°). This prevented subjects from holding a representation of a single fixed point as the true center of all squares. In condition 1 (Squaremark task, SM), the squares were marked centrally (in 40% of trials) or not (in the remaining 60% of trials). If the mark was not central, the misplacement was either 0.75° or 1° to the left, right, up, down, left and up, right and up, left and down or right and down (in equal proportions) of the center. In condition 2 (control task for Squaremark task, SC), the same squares but with no mark in the center were shown in 60% of the trials. In the remaining 40% of trials, squares with a mark (as described above) were presented. In conditions 3 and 4, horizontal lines of length corresponding to a visual angle of 10° or 12° were presented in each screen quadrant. In condition 3 (Landmark task, LM), the lines were either correctly (in 40% of trials) or incorrectly (in the remaining 60% of trials) pre-bisected by a small vertical mark. If this mark was not central, the misplacement was either 0.75° or 1° to the left or right of the center. In condition 4 (control task for the Landmark task, LC), the same lines but with no mark were shown in 60% of the trials. In the remaining 40% of trials, lines with marks were presented. In all conditions, a block of trials consisted of a total of 40 stimuli, each condition lasting 60 s. In between conditions a 20 s 'baseline' was introduced to allow for a 5 s presentation of the task instructions to the subjects. This was followed by a white screen with a black circle (diameter of 20°) in the center of the screen for 15 s. In this way, we prevented an overlap of neural activity specific to the experimental conditions and hence allowed the haemodynamic responses to be separated. Each of the four conditions (block of trials) was presented to each subject once per experimental run. Experimental runs were repeated five times per subject.

In SM, subjects judged whether or not the presented square was marked at its center. Response was by right index finger button press if the square was marked at its center and by right middle finger press of another button if the square was marked elsewhere. In SC, subjects judged whether or not the presented square had a mark in it. Response was by right index finger

button press if there was a mark in the square and by right middle finger button press if there was no mark. In LM, subjects judged whether or not the presented horizontal line was correctly bisected. Again, response was by right index finger button press if the line was correctly bisected and by right middle finger button press if the line was incorrectly transected. In LC, subjects judged whether or not each horizontal line had a mark on it. Again, subjects pressed a button with their right index finger if the line had a mark and another button with their right middle finger if there was no mark. Reaction times and error rates were recorded.

2.2. Eye movements and eye movement data analysis

All tasks were performed in free vision for the following reasons. First, the clinical versions of the Landmark and Squaremark tasks are so performed. Second, we have previously demonstrated that there is a strong interaction between the neural activity resulting from an object-centered visuo-spatial information processing task and allowing/disallowing eye movements [5]. To test for putative differential eye movements in the experimental conditions, we conducted an eye movement study (using an infra-red on-line monitoring video-based eye tracking device) on all subjects after the imaging study: We did not want subjects to be overly practiced before scanning commenced.

Eye position was analyzed using the normalized x- and y-coordinates of the subject's gaze on the screen. For each of the four conditions, we analyzed the length of the total scan path and the overall time subjects kept their gaze in the proximity of the visual stimuli within each of the screen quadrants. The mean values of each condition were compared by ANOVA.

2.3. fMRI hardware and procedures

Functional MR images were acquired on a Siemens Vision 1.5T whole-body scanner using standard imaging procedures (Gradient-echo EPI, TE = 66 ms, TR = 5 s, flip angle = 90°, 30 slices of 4.00 mm thickness each, inter-slice gap 0.4 mm, FOV = 200 mm, in-plane resolution = 3.125 × 3.125 mm) as described [6]. The fMRI paradigm consisted of a baseline of 35 s (7 × TR) followed by four repetitions of a cycle with a 60 s activation period (12 TR) and a 20 s (4 TR) baseline period.

2.4. Image processing and statistical analysis

Images were realigned and normalized into standard stereotactic space (resulting pixel size 4 × 4 × 4 mm) [8,9]. For the group analysis, the transformed functional images were then smoothed with a Gaussian kernel of 10 mm (FWHM) to meet the statistical requirements of the GLM and to compensate for normal variation in anatomy across subjects [9]. For statistical analysis, low frequency cosine waves modeled and removed subject-specific low frequency drifts in the signal, and global means were normalized by proportional scaling. The different data sets were modeled as reference waveforms (i.e. box car functions convolved with a haemodynamic response function [7]). Repeated measures (scans) were collapsed within subjects to give one scan per condition per subject per experimental run. The conditions were compared between subjects, effecting a random effects model that allows inference to the general population. This analysis, rather than fMRI single subject approaches, was adopted as the current study investigates a neuropsychological hypothesis derived from lesion studies in patient populations. Accordingly, we did not intend to study variability from subject to subject in how these judgement tasks were performed. Rather, we wanted to image the relevant areas held in common across a sample of normal subjects. This random effects analysis precludes reporting time courses of the haemodynamic responses as repeated measures (scans) are collapsed.

Specific effects were tested by linear contrasts of the parameter estimates for each condition, resulting in t-statistics which, after transformation to Z-statistics, constituted statistical parametric maps (SPM) interpreted by referring to the probabilistic behavior of Gaussian random fields. The data were first analyzed for activations common to all experimental conditions relative to the baseline by means of a conjunction analysis [25]. Next, the main effects of task (SM + LM > SC + LC; SC + LC > SM + LM) and stimuli (SM + SC > LM + LC; LM + LC > SM + SC) assessed the functional anatomy common to one- and two-dimensional positional judgements relative to the control tasks (and vice versa), and the differences in neural activations resulting from the stimuli used. Voxels were identified as significant only if they passed a height threshold of $Z = 4.5$ ($P < 0.05$, corrected for multiple comparisons) and belonged to a cluster of at least 50 activated voxels [9]. These stringent criteria were adopted in order to minimize the possibility of false positives (type II error).

Only half the total number of scans from each subject are relevant to the simple main effects of task (SM > SC; LM > LC). Hence, there was only half the total number of observations that had been entered into the statistical analysis of task and stimuli. Accordingly, the statistical threshold was reduced to $P < 0.001$ (uncorrected) for the simple main effects. Finally, the data were analyzed for the interaction of task and stimuli (SM–SC > LM–LC and vice-versa). The statistical threshold for the interactions was set at $P < 0.005$ as we interrogated only those activations observed as simple

main effects in order to assess whether or not those activations were indeed significant differential activations between SM and LM. The stereotactic coordinates of the local maximum within areas of significant relative activity change were assessed by reference to the standard stereotactic atlas [29]. This atlas also provides a correlation between Brodmann areas (BA) and stereotactic coordinates. However, it should be kept in mind that the Brodmann maps do not reflect the complete cytoarchitectonic organization of the human brain. Likewise, the macroscopic landmark-based transformations of the schematic Brodmann map to the Talairach brain does not guarantee the precise localization of areal borders in the stereotactic atlas [26,37]. Nevertheless, the approximate correlation with Brodmann areas is given in Tables 1 and 2 for the convenience of readers used to the Brodmann parcellation scheme.

3. Results

Significant increases in neural activity ($P < 0.05$, corrected) common to all four conditions relative to baseline were observed in networks concerned with visual stimulation and analysis (complete occipital cortex and temporo-occipital transition), visuo-spatial attention (superior and inferior parietal lobules and thalamus), decision making (lateral premotor and supplementary motor cortices), visuo-motor coordination (cerebellum and striatum) and response execution (primary motor and somatosensory cortices). Table 1 summarizes the local maxima and the Z-scores within these regions.

Significant increases in neural activity during both two-dimensional square center judgements and one-dimensional horizontal line center judgements relative to the respective two- and one-dimensional control tasks ($SM + LM > SC + LC$; $P < 0.05$ corrected) were observed only in lateral inferior occipital cortex bilaterally. The reverse comparison did not reveal any significant activations. The areas activated as a main effect of task are displayed in Fig. 1(a); the local maxima and Z-scores are summarized in Table 2(a).

Increased neural activity associated with squares (relative to lines), irrespective of which task was performed ($SM + SC > LM + LC$; $P < 0.05$, corrected) was observed only in lateral and medial occipital cortex bilaterally and most likely reflected the more extensive visual input: The reverse comparison did not show any significant activations associated with horizontal lines (relative to squares). The areas activated as a main effect of stimuli are depicted in Fig. 1(b); the local maxima and Z-scores are summarized in Table 2(b).

As hypothesized, increases in neural activity associated with the square center judgements ($SM > SC$; $P < 0.001$) were observed in ventral posterior brain regions. No significant increases (relative to the square control) were observed in either the superior or inferior parietal cortex. Table 2(c) summarizes the areas of increased neural activity, which are illustrated in Fig. 1(c).

Table 1
Relative increases in brain activity during performance of the Landmark task, the Squaremark task and the control tasks[a]

Region	Side	x	y	z	Z-score
All task and control conditions relative to baseline: (conjunction analysis of SM > baseline, SC > baseline, LM > baseline, LC > baseline)					
Primary motor cortex (BA 4)	L	−42	−12	+48	8.2
Primary somatosensory cortex (BA 3,1,2)	L	−50	−26	+36	5.9
Supplementary motor area (mesial part of BA 6)	L	−6	+2	+48	5.7
Cerebellar hemisphere	R	+24	−52	−28	6.9
	L	−30	−54	−36	5.9
Cerebellar vermis	M	+2	−74	−40	5.3
Primary visual cortex (BA 17)	M	+2	−88	+4	5.4
Lateral temporo-occipital cortex (BA 18/19 and 21/37)	L	−42	−68	−2	6.3
	R	+48	−60	−8	4.9
Thalamus	L	−12	−12	+2	5.8
Striatum	L	−28	+2	0	4.7
Lateral premotor cortex (BA 6)	R	+42	−4	+50	5.8
Inferior parietal cortex (BA 40)	R	+30	−46	+40	5.5
	L	−36	−38	+50	5.6
Superior parietal cortex (BA 7)	R	+30	−52	+50	4.6
	L	−34	−50	+56	5.3

[a] Coordinates are in standard stereotactic space [29] and refer to maximally activated foci as indicated by the highest Z-score within an area of activation associated with all task and control conditions relative to baseline (conjunction analysis of SM > baseline, SC > baseline, LM > baseline, LC > baseline). For each area of activation, an estimate of the Brodmann area (BA) is given in parentheses, which is based on the stereotactic atlas of Talairach and Tournoux [29]. x is the distance in millimeters to the right (+) or left (−) of the midsagittal (interhemispheric) line; y is the distance anterior (+) or posterior (−) to the vertical plane through the anterior commissure; and z is the distance above (+) or below (−) the intercommissural line. R, right; L, left; M, medial; SM, Squaremark task; SC, control task for Squaremark task; LM, Landmark task; LC, control task for Landmark task.

Table 2
Relative increases in brain activity associated with the visuo-spatial judgement tasks and the stimuli used[a]

Region	Side	x	y	z	Z-score
(a) Main effect of task: (SM+LM)>(SC+LC)					
Lateral inferior occipital cortex (BA 18)	R	+34	−92	−2	5.7
	L	−30	−92	−2	5.2
(b) Main effect of stimuli: (SM+SC)>(LM+LC)					
Lateral occipital cortex (BA 17/18)	R	+22	−94	+12	4.8
	L	−16	−98	+4	4.3[b]
Medial occipital cortex (BA 17/18)	M	+6	−82	−12	4.6
(c) Simple main effect of Squaremark task: SM>SC					
Lingual gyrus (BA 19)	L	−8	−58	−6	4.4*
	R	+18	−54	−6	4.2*
Lateral inferior occipital cortex (BA 18)	L	−30	−92	0	4.3
	R	+32	−94	−2	4.1
Superior occipital cortex (BA 19)	R	+16	−78	+32	3.4
Lateral temporo−occipital cortex (BA 19/39)	R	+44	−80	+18	3.3
(d) Simple main effect of Landmark task: LM>LC					
Lateral inferior occipital cortex (BA 18)	R	+36	−90	−2	4.3
	L	−34	−88	−8	3.6
Medial superior occipital cortex (BA 18)	R	+16	−72	+18	3.5
Cerebellar hemisphere	L	−34	−54	−32	4.0
Inferior parietal cortex (BA 40)	R	+40	−50	+56	3.1**

[a] For abbreviations see Table 1.
[b] The activation of left occipital cortex as a main effect of stimuli just fails to survive correction ($Z = 4.5$, $P < 0.05$ corrected).
* Interaction testing for differential activation (relative to Landmark task) significant.
** Interaction testing for differential activation (relative to Squaremark task) significant.

Table 2(d) summarizes the areas with increases in neural activity associated with line center judgements (LM > LC; $P < 0.001$). As expected (on the basis of our previous functional imaging study of the Landmark task [6]), significant increases in neural activity associated with the Landmark task (relative to the line control) were observed in lateral inferior and medial superior occipital cortex bilaterally, the left cerebellar hemisphere and the right inferior parietal cortex. Fig. 1(d) illustrates the local maximum in the depth of the right intraparietal sulcus. The area of parietal activation included cortex on the right parietal convexity as well as in the branches of the right intraparietal sulcus. Activations that were not predicted by our previous functional imaging study of the Landmark task [6] were observed in the inferior anterior cingulate cortex, the right anterior insular cortex and the right lateral premotor cortex. As these areas did not survive a statistical threshold for multiple comparisons, they are not further considered here. We nonetheless note that lesion to these areas can give rise to visuospatial neglect, albeit less frequently than the lesion of the inferior parietal lobule [33].

As the simple main effects for the square center and line center judgements suggested differential activations between the two tasks, the significance of these differences was assessed by analysis of the interaction terms. This interaction confirmed the significance of the differential activations in the right intraparietal sulcus associated with the Landmark task ($P < 0.005$, $Z = 2.9$) and in the lingual gyrus bilaterally associated with the Squaremark task ($P < 0.001$, $Z = 3.2$).

There were no significant differences in eye movements across conditions. The mean scan path and the mean time spent in the proximity of the visual stimuli were not significantly different between the Squaremark task, the Landmark task and the respective control conditions. Reaction times (RT) taken outside the MR scanner during the eye movement study demonstrated that subjects were significantly quicker when responding to the control conditions than to the Squaremark and Landmark conditions [$F(1,44) = 10.1$, $P = 0.003$] Table 3. RTs taken inside the scanner during the fMRI study revealed a similar advantage [$F(1,40) = 7.15$, $P = 0.01$] for the control conditions (SC: 479 ± 31 ms; LC: 485 ± 39 ms) relative to the Landmark (LM: 552 ± 90 ms) and Squaremark tasks (SM 514 ± 72 ms). No significant differences in error rates were observed between conditions. The S.D.s of the behavioural measures are relatively small and hence suggest that individual variation in task performance is not a major issue in this study. This, in turn, supports our use of the random effects model for the imaging results.

4. Discussion

The areas activated differentially during the line center judgements (right inferior parietal cortex) are consistent with our own previous fMRI study [6], a major clinical/CT correlation study [34] and a recent CT and SPECT report that the right supramarginal gyrus may be the 'most significant parietal subregion' involved in hemispatial neglect [19]. The right inferior parietal region, activated here by line center judgements, is distinct from the more superior parieto-occipital areas implicated in a recent fMRI study of the 'egocentric spatial frame of reference' [35]. In that report, subjects pressed a button when a vertical bar, moving horizontally, was judged to cross the observer's midsagittal plane [35]. In our study, we presented the stimuli in the four quadrants of the visual field in order to prevent subjects from using a subjective radial projection of their midsagittal plane ('straight ahead') to estimate the center of the stimuli. That the two studies give rise to distinct regions of activation in parietal cortex indicates that subjects in our study used stimulus-centered coor-

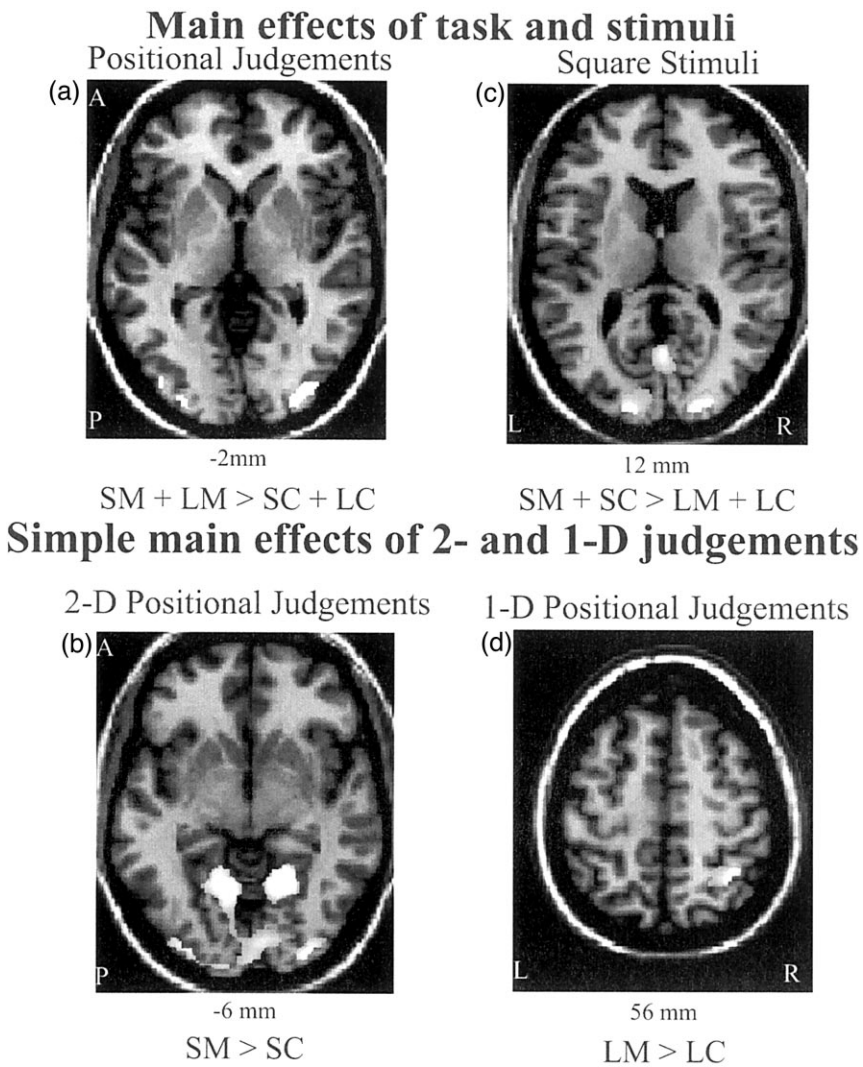

Fig. 1. Relative increases in neural activity (for the 12 subjects) associated with: (a) two-dimensional square center judgements and one-dimensional horizontal line bisection judgements relative to the respective two- and one-dimensional control tasks ($SM + LM > SC + LC$; $P < 0.05$ corrected); (b) squares relative to horizontal lines ($SM + SC > LM + LC$; $P < 0.05$ corrected), (c) two-dimensional square center judgements relative to the respective two-dimensional control task ($SM > SC$; $P < 0.001$); and (d) one-dimensional horizontal line bisection judgements relative to the respective one-dimensional control task ($LM > LC$; $P < 0.001$). The local maxima of the areas of significant relative increase in neural activity are displayed superimposed on transverse MR sections to detail the functional anatomy of the activations. There is bilateral lateral inferior occipital cortex activation with one- and two-dimensional visuospatial judgements (a), lateral and medial occipital cortex activation bilaterally with squares (b), activation of the lingual gyrus and the inferior occipital cortex bilaterally with two-dimensional visuospatial judgements (Squaremark task, c), and right hemispheric neural activation centered on the intraparietal sulcus during one-dimensional visuo-spatial judgements (Landmark task, d). The exact coordinates of the local maxima within the areas of activation and their Z statistics are given in Table 2. R, right; L, left; A, anterior; P, posterior.

Table 3
Behavioral measures during performance of the Squaremark task and the Landmark task: Reaction times, error rates, and scan path (taken from the eye movement study performed outside the MR scanner)[a]

	Task				Level of significance	
	LM	SM	LC	SC	LM+SM > LC+SC	Squares versus horizontal lines
RT (ms)	643 (±72)	603 (±79)	543 (±88)	547 (±98)	0.005	n.s.
Errors (%)	1.5 (±1.2)	1.1 (±0.7)	1.1 (±0.6)	1.1 (±0.8)	n.s.	n.s.
Scan path (pixels)	23514 (±3197)	23598 (±2904)	22363 (±2549)	22162 (±2693)	n.s.	n.s.

[a] RT, reaction time; Scan path, number of pixels traversed.

dinates, not egocentric coordinates when judging the center of the stimuli.

Areas activated differentially during square center judgements (the lingual gyrus bilaterally) are ventral stream visual brain regions that form part of the 'what' system [31] activated during visual form [17,28] and object processing [3,13]. Our data strongly suggest that areas within the 'what' system are also involved in visuo-spatial operations. The alternative explanation that activation of these areas results from increased visual attention [2,4] seems unlikely: 'Top-down' attentional gating was assessed by the main effect of task which shows activation of lateral inferior occipital cortex. Two other functional imaging studies on object-centered visuospatial processing support the involvement of ventral stream areas in spatial tasks [5,16].

Other behavioral data also suggest that one- and two-dimensional spatial judgements are cognitively and neuropsychologically distinct. For example, normal subjects can make finer discriminations between rectangles of different heights than between vertical lines of the equivalent extent [1]. Likewise, it has been demonstrated that men with penetrating missile injuries to posterior brain regions could not distinguish between lines of 5 and 8 cm, but could nonetheless accurately judge that oblongs, in which the pairs of opposing sites were 4.2 and 4.5 cm, were not squares [15]. When one patient had 'to decide whether a figure was a square he did not compare the lengths of its sides' but rather reported that 'on the first glance I see the whole figure and know whether it is a square or not' [15]. The authors concluded 'it is therefore obvious that though he could not compare or estimate linear extensions he preserved the faculty of appreciating the shape of bidimensional figures' [15]. Our results extend such findings by providing a functional basis for one-dimensional positional judgements in the right inferior parietal cortex and for two-dimensional positional judgements in the lingual gyri bilaterally. Stimulus-configuration thus appears to interact with the nature of the judgement itself in determining the principal cerebral loci implicated in task performance. The more the stimulus approximates to a good gestalt [10], the greater the role played by the ventral route in assessing position within the object. This conjecture in turn suggests an explanation for why left neglect on bisection tasks progressively diminishes as a stimulus line is progressively expanded through rectangles to a square [11,30]. Exactly why a square should be more 'object'-like than a line is an issue that demands further inquiry. One possibility is that the visual system treats very 'thin' stimuli (e.g. a line) as more like edges than objects. By contrast, even an outline square may be more likely to evoke the percept of the surface of an object [23].

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